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DIFFERENTIAL WINTER DISTRIBUTION OF ROUGH-LEGGED HAWKS (*BUTEO LAGOPUS*) BY SEX IN WESTERN NORTH AMERICA

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ABSTRACT.—We conducted roadside surveys of Rough-legged Hawks (*Buteo lagopus*) in Montana, California, and Nevada for four consecutive winters from 1995–96 through 1998–99. The proportion of adult males to adult females and of adults to juveniles in the samples did not change significantly throughout the winter at any location. Adult females outnumbered adult males on all but one survey in Montana, and adult males outnumbered adult females on every survey in California and Nevada. The mean ratio of males to females was significantly lower in Montana than in the southerly locations, suggesting that on average, females wintered farther north than males. Furthermore, the annual mean percentage of adult females at all locations was correlated with average temperature and snowfall. The ratio of adults to juveniles did not differ significantly between locations within a year, suggesting there was no differential winter distribution by age. However, the proportion of juveniles in each location varied significantly among years. The sex ratio of juvenile Rough-legged Hawks trapped in Montana was nearly identical to ratios observed for adults on road surveys. Sex ratios of 63 museum specimens provided further evidence that, on average, female adult and juvenile Rough-legged Hawks winter farther north than do males. We reviewed three hypotheses for latitudinal segregation of the sexes and suggest that thermal regulation is an important factor influencing differential winter distribution in Rough-legged Hawks.

KEY WORDS: Buteo lagopus; *Rough-legged Hawk*; *roadside raptor surveys*; *winter distribution*; *latitudinal segregation*; *differential migration.*

Distribución diferencial por sexo de *Buteo lagopus* al pasar el invierno en el oeste de Norteamerica

RESUMEN.—Llevamos a cabo conteos de carretera de *Buteo lagopus* en Montana, California, y Nevada por cuatro inviernos consecutivos desde 1995–96 hasta 1998–99. La proporción de machos adultos en relación a hembras adultas y de adultos a juveniles en la muestra no varió significativamente a través del invierno en ninguna localidad. Las hembras adultas sobrepasaron a los machos adultos en todas las localidades exceptuando a Montana y los machos adultos sobrepasaron a las hembras adultas en cada monitoreo en California y Nevada. La proporción media de machos a hembras fue significativamente más baja en Montana que en las localidades del sur, lo que sugiere que en promedio, las hembras pasaron el invierno más al norte que los machos. Aún más, el porcentaje de la media anual de hembras adultas en todas las localidades fue correlacionado con la temperatura promedio y la precipitación de la nieve. La proporción de adultos y juveniles no difirió significativamente entre localidades entre años, lo cual sugiere que no existió una diferencia por edades de la distribución de individuos que pasan el invierno en este sitio. Sin embargo, la proporción de juveniles en cada localidad varió significativamente entre años. La proporción de sexos de 63 especímenes de museo provee evidencias de que en promedio las hembras adultas y los juveniles de *Buteo lagopus* pasan el invierno más al norte que los machos. Resumimos tres hipótesis para la segregación latitudinal por sexos y sugerimos que la regulación térmica es un factor importante que influye en la distribución diferenciada de *Buteo lagopus*.

[Traducción de César Márquez]

Rough-legged Hawks (*Buteo lagopus*) are Holarctic raptors that, in the western United States and Canada, winter from southern British Columbia and Alberta, south through California and New Mexico (American Ornithologists' Union 1998). As do all North American buteos, they exhibit reversed sexual size dimorphism, with females being larger than males. Several studies have provided evidence of differential winter distribution (Russell 1981, Kjellén 1994). Kjellén (1994) studied migrant and wintering Rough-legged Hawks in Sweden and found significantly more adult females and juveniles among wintering birds than among southbound migrants in autumn, although this was not consistent for every year of the study. Russell (1981) examined Rough-legged Hawk specimens collected from mid-December–mid-February in the eastern United States and found that females predominated in the north and males were more numerous in the southern portion of the range. However, he did not determine the age of specimens. Contrary to Kjellén (1994), Mindell in Palmer (1988) reported that juvenile Rough-legged Hawks tend to migrate farther south than adults in North America.

Several hypotheses have been proposed to explain differences in winter distribution between sex and age classes in birds. The arrival-time hypothesis suggests that the sex which establishes the territory (usually males) should winter closest to the breeding grounds (King et al. 1965, Myers 1981, Wallin et al. 1985, Kjellén 1994). The social-dominance hypothesis proposes that subordinates which cannot compete successfully for resources with dominant birds migrate farther south or use suboptimal habitats (Gauthreaux 1985, Kerlinger and Lein 1986). The body-size hypothesis asserts that because of thermal advantages, larger individuals winter farther north than smaller individuals (Ketterson and Nolan 1976, Searcy 1980).

The purpose of our study was to determine the age and sex ratios of Rough-legged Hawks wintering in western North America within, between, and among winters to better understand their winter distribution. Furthermore, we wanted to explore the possible causal effects of the observed sex and age distributions.

STUDY AREAS AND METHODS

This study was conducted in the Mission Valley, Montana (47°50′N, 114°25′W), Sierra Valley, California (39°60′N, 120°25′W), and Lovelock Valley, Nevada (40°25′N, 118°50′W) (Fig. 1). Study sites were chosen because of their abundance of wintering raptors. The Mission Valley is in the northern portion of the winter range of the Rough-legged Hawk. Land use in these areas is predominately agriculture and livestock grazing. The Sierra and Lovelock valleys are 1130 km and 960 km farther southwest, respectively, in the mid to southern portion of the Rough-legged Hawk's winter range (see Palmer 1988). Each of these valleys has an extensive system of secondary roads with limited vehicular traffic and numerous utility poles and fence posts that are used by perching hawks.

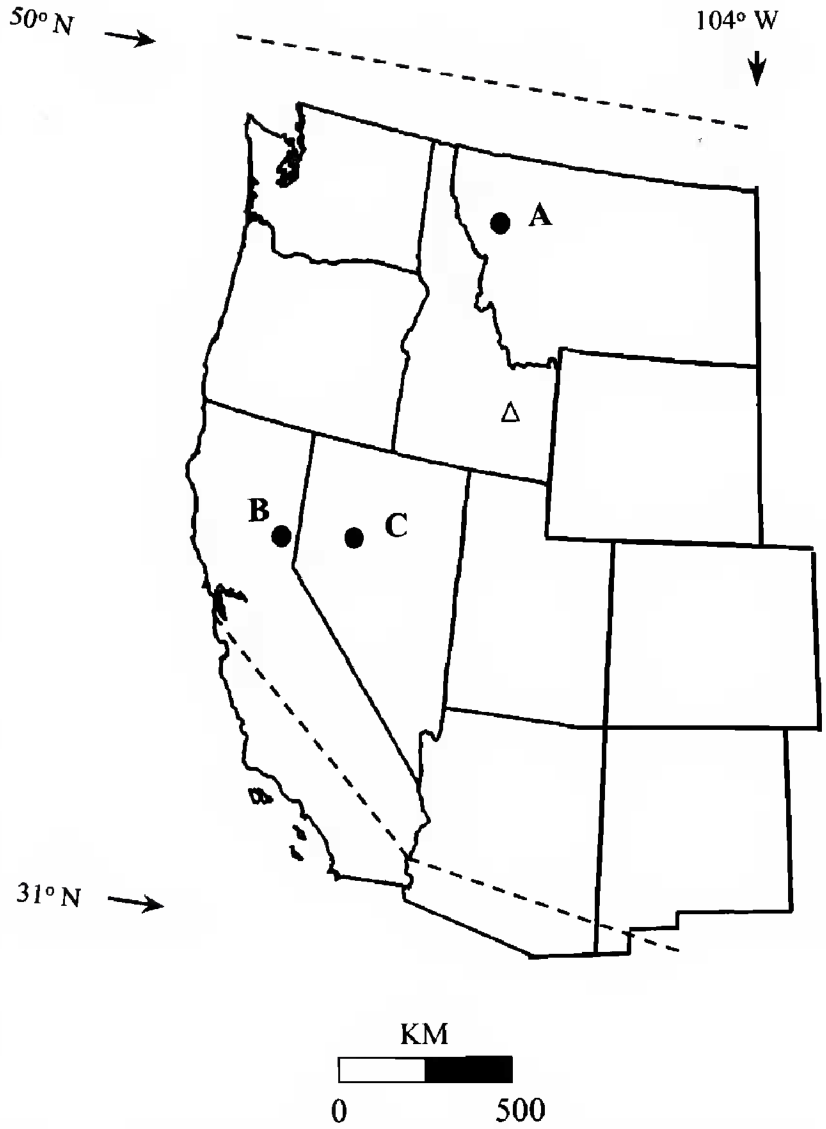

Figure 1. Mission Valley, Montana (A), Sierra Valley, California (B), and the Lovelock Valley, Nevada (C) study sites in the western United States. Also shown is Watson's (1984) study site in Idaho (open triangle) and approximate northern and southern extent of Rough-legged Hawk wintering range (shown by dashed line; Palmer 1988).

The Mission Valley (40 × 20 km) is in west-central Montana approximately 65 km north of Missoula at an elevation of about 800 m. The Sierra Valley (30 × 15 km) is in the Sierra Nevada Mountains, California, approximately 40 km northwest of Reno, Nevada, at an elevation of about 1500 m. The Lovelock Valley (30 × 20 km) is 145 km northeast of Reno, Nevada, at an elevation of approximately 1200 m.

We conducted 27 roadside surveys from November through April during four consecutive winters from 1995–99, hereafter referred to as winters one through four. Of these, 21 were conducted in Montana (i.e., northern location), and 6 in California and Nevada (i.e., southern locations). One transect was surveyed monthly in the Mission Valley during each winter except the first, during which two transects were surveyed simultaneously (by two groups of observers). The survey day varied among winters one through four; surveys were conducted near the beginning of the month during winters one and two, and on day 20 of each month during winters three and four. The two transects in the Mission Valley were 63 and 60 km long, respectively. The 60-km transect was abandoned after the first winter, and the longer transect was reduced to the last 43.5 km after the first survey of the second winter because of time restrictions. Thereafter, the 43.5-km transect was surveyed consistently. One 73-km transect was surveyed monthly in the Sierra Valley the second winter, and opportunistically the third and fourth winters. Finally, one 48-km transect was surveyed in the Lovelock Valley, Nevada, during the first and second winters (both in January).

Surveys began between 0830–1030 H, depending on the time of year, to allow enough time for hawks to disperse from roost sites to foraging areas. Each transect was surveyed by two observers in one vehicle traveling at a continuous speed of 25–35 kph and took 2.5–4.5 hr to complete depending on the number of birds sighted. Observers stopped the car to determine the age and sex of each bird sighted. All birds were initially detected without the use of optics, after which binoculars and 15–45× spotting scopes were used for species identification and determination of age and sex. The sex, age, activity, distance from observer, location, and time were recorded for every Rough-legged Hawk sighted. Multiple features were used for determining sex and age based on Cade (1955), Clark and Wheeler (1987) and Wheeler and Clark (1995). Juvenile Rough-legged Hawks cannot be sexed by plumage, so sex determination was confined to adults. Any uncertainty in the identification of sex or age was recorded as "unknown."

In addition to doing road surveys, we also obtained the sex ratios of Rough-legged Hawks collected throughout the western U.S. (west of 104°W) from various museums (see acknowledgments for list of museums). We limited the analysis to specimens collected between 1 December–28 February to minimize the number of migrating birds in the sample. To examine whether a latitudinal gradient existed, we divided the specimens into three latitudinal ranges: 31°–40°, 41°–46° and 47°–49°N.

For assessing the sex ratio of juvenile Rough-legged Hawks, we inspected trapping data from Montana. As part of a separate study, Rough-legged Hawks were trapped, banded, and radiotagged each winter in Montana since 1995. The age and sex of each hawk was determined using plumage characteristics, iris color, and body measurements. Also, for investigating social interactions, we conducted extensive behavioral observations on radio-tagged birds in Montana, recording all intraspecific and interspecific interactions. All interactions involving noninstrumented birds were also recorded. A bird was described as "winning" an interaction if it: (1) successfully displaced another bird from a perch or from the immediate "air space" (Bildstein 1987) or (2) successfully defended a perch or "air space" when challenged by another bird. Thus, the frequency of "winning" interactions considered both the instigator and the recipient.

We used a chi-square test to evaluate differences between sex and age ratios throughout each winter at a location. Because survey data were analyzed as proportions, they were arcsine transformed (Wilkinson et al. 1996). Differences in sex and age ratios between and among years and among locations were tested with ANOVA and Tukey's pairwise comparisons using SYSTAT 7.0 (Wilkinson et al. 1996). The survey conducted the first winter was not included in the statistical analysis because it was the only survey done in a southern location that year. Additionally, because survey results from California and Nevada were nearly identical, they were combined and are heretofore referred to as southern surveys. Five surveys were excluded from the analysis because fewer than seven hawks were detected. Two other surveys attempted in California were abandoned because of poor visibility, and two surveys were not included in the analysis of age ratio because they were diagnosed as outliers.

Climatological data for the Mission Valley were obtained from the Western Regional Climate Center. We tested for correlations between sex ratio and climatic differences between and among years using the Pearson correlation. We did not compare climatological data with the southern locations because of the lower number of surveys and inconsistency of survey dates. A one-sided Mann-Whitney U procedure was used for testing whether female specimens were recovered farther north than males for the museum specimens. Finally, data were checked for skewness, normality, outliers, homogeneity of variances, and auto-correlation (Wilkinson et al. 1996).

RESULTS

We detected more adult males than females on all surveys in the southern locations, and more adult females than males on all surveys in the northern location, except for one in February of the third winter (Table 1). The proportion of adult males to adult females did not vary significantly throughout a winter in any location (Chi-square test; $P > 0.05$); however, the sex ratio was significantly different between the northern and southern locations within and among winters (Table 2). The proportion of females detected on surveys in the northern location was significantly lower in the third winter compared with the first but did not differ significantly between any consecutive winters (Table 2). However, the mean percentage of adult females was significantly inversely correlated with average temperature ($r = -0.982$, df = 3, $P = 0.018$) and less strongly correlated with average snowfall ($r = 0.901$, df = 3, $P = 0.099$) among winters in Montana.

The proportion of adults to juveniles did not vary significantly within any winter in any location (Chi-square test; $P > 0.05$) (Table 3); however, the

Table 1. Percentage of adult female Rough-legged Hawks (number of adults in parentheses) detected on surveys in northern (N = Montana) and southern (S = Nevada and California) locations during four consecutive winters (1–4) from 1995–96 through 1998–99. Climatic data shown at the bottom of the table include the average deviation from monthly normal, averaged for each winter.

	MONTANA				CALIFORNIA			
MONTH	N1	N2	N3	N4	S1	S2	S3	S4
Nov.	69	62	57	70		20	33	33
	(13)	(29)	(14)	(46)		(5)	(9)	(3)[a]
Dec.	80		65	60		29		
	(10)		(26)	(42)		(7)		
Jan.	79	77	61	55	11	20		0
	(19)	(13)	(31)	(56)	(9)[b]	(5)		(1)[a]
Feb.	77		49	63		33		
	(22)		(35)	(35)		(12)		
Mar.	73	75	67	74		0	29	
	(11)	(12)	(33)	(39)		(2)[a]	(7)	
Apr.	71	73	100	67		100		
	(7)	(22)	(1)[a]	(6)		(1)[a]		
Mean % ± SD	75 ± 4	72 ± 7	60 ± 7	65 ± 5	11 ± 0	27 ± 7	31 ± 3	
Ave. temp (C°)[c]	−0.86°	−0.51°	+2.8°	+3.1°				
Snowfall (cm)[c]	+3.6	+9.4	−14.3	−6.3				

[a] Survey not included in analysis because fewer than 7 hawks were detected.

[b] Survey not included in analysis because it was the only one done in a southerly location the first year.

[c] Average monthly deviation from 90-year climate averages, Nov.–Feb., recorded at St. Ignatius, Montana by the Western Regional Climate Center.

age ratio differed significantly between and among most winters in each location (Table 4). Still, the age ratio was not significantly different between northern and southern locations within a winter (Table 4). Additionally, the average percentage of adults among winters in Montana was not correlated with differences in average temperature (P = 0.89) or snowfall (P = 0.53). Finally, the number of Rough-legged Hawks (birds/km) differed greatly between the first winter and all remaining winters in Montana, but numbers fluctuated considerably less among years in California (Table 3).

Table 2. Pair-wise mean comparison (ANOVA, Tukey's method) of sex ratio between northern (N) and southern (S) locations in winters 1–4 (1995–99). Sex ratios of male and female Rough-legged Hawks differed significantly between northern and southern locations both within and among winters.

	N1	N2	N3	N4	S2	S3
N1	1.00					
N2	0.97	1.00				
N3	0.01*	0.10	1.00			
N4	0.11	0.55	0.79	1.00		
S2	0.00**	0.00**	0.00**	0.00**	1.0	
S3	0.00**	0.00**	0.00**	0.00**	0.9	1.0

* Significant at 0.05 alpha level.

** Significant at 0.001 alpha level.

The proportion of hawks per survey where the age, sex, or both, were unknown averaged 12% ± 1 (±1 SE, range = 0–35%). We had a lower number of unknown hawks on surveys that recorded the greatest number of individuals, as well as on sunny days when hawks tended to soar in thermals.

Of the 65 museum specimens examined, we found that females were recovered significantly farther north on average than males (one-sided Mann-Whitney U, P = 0.019, ages not distinguished, Table 5). Furthermore, the sex ratios were similar to those recorded on road surveys at equivalent latitudes. The three lowest latitude specimens were males (min ≈31°; a juvenile male collected near El Paso, Texas), and the four specimens collected from the highest latitude (≥48°) were all females. Additionally, the mean latitude for male and female specimens was 43° N ± 4.2 and 45° N ± 2.8, respectively.

Table 3. Percentage of adult Rough-legged Hawks (number of hawks in parentheses) detected on surveys in northern (N = Montana), and southern (S = Nevada and California) locations during four consecutive winters (1–4) from 1995–96 through 1998–99. Also, average number of Rough-legged Hawks/km (i.e., hawk density) on survey route for November–February surveys each winter.

	Montana				California			
Month	N1[a]	N2	N3	N4	S1	S2	S3	S4
Nov.	100 (13)	62 (47)	74 (19)	87 (53)		63 (8)	82 (11)	50 (6)[b]
Dec.	100 (10)		81 (32)	78 (54)		58 (12)		
Jan.	86 (22)	45 (29)	79 (39)	78 (72)	75 (12)[c]	71 (7)		100 (1)[b]
Feb.	92 (24)		83 (42)	70 (50)		60 (20)		
Mar.	65 (17)[d]	50 (24)	89 (37)	80 (54)		67 (3)[b]	88 (8)	
Apr.	87 (8)	69 (32)	33 (3)[b]	40 (15)[d]		100 (1)[b]		
Mean % ± SD	88 ± 13	56 ± 11	81 ± 6	72 ± 16	75	63 ± 6	85 ± 4	75
RLHAs/km	0.33	1.1	0.86	1.4	0.25	0.16	0.15	0.05

[a] Sum of two transects.
[b] Survey not included in analysis because of the low number of hawks detected.
[c] Survey not included in analysis because it was the only one done in a southerly location the first year.
[d] Survey not included in analysis because it was diagnosed as an outlier.

We trapped 55 Rough-legged Hawks in Montana from 1995–99 (20 adults and 35 juveniles). Overall, 55% of adults and 77% of juveniles were female, based on measurements (Table 6). The number of juvenile females trapped outnumbered juvenile males every year; however, adult females only outnumbered adult males in the third and fourth winters (Table 6). For juveniles, the average proportion that was female was 76.6% and ranged among winters from 83.3% (1995–96) to 66.7% (1998–99).

We recorded 171 intraspecific and 85 interspecific interactions while tracking and observing 17 (7 adults, 10 juveniles) instrumented hawks during the winters of 1997–98 and 1998–99. Thirteen percent of 123 intraspecific interactions between known-age birds involved adult females displacing adult males, compared with <1% where adult males displaced adult females (Table 7). However, interactions between and within other age and sex

Table 4. Pair-wise mean comparisons (ANOVA, Tukey's method) of age ratio between northern (N) and southern (S) locations in winters 1–4 (1995–99). Age ratio differed significantly between northern and southern locations between and among most winters, but were not significantly different within a winter (shown in bold).

	N1	N2	N3	N4	S2	S3
N1	1.00					
N2	0.00**	1.00				
N3	0.08	0.01*	1.00			
N4	0.03*	0.01*	0.99	1.00		
S2	0.00**	0.95	0.03*	0.08	1.00	
S3	0.34	0.02*	1.00	0.99	0.10	1.00

* Significant at 0.05 alpha level.
** Significant at 0.001 alpha level.

Table 5. Sex composition of Rough-legged Hawk specimens collected from different latitudes between 1 December–28 February, and west of 104°W longitude in the western United States (see Acknowledgments for list of museums).

Latitude (°N)	*N*	% Females
47°–49°	25	68 (17)
41°–46°	24	62 (15)
31°–40°	16	31 (5)

Table 6. Age and sex composition of Rough-legged Hawks trapped in the Mission Valley, Montana (Olson unpubl. data).

	Sex Ratio (M:F)	
Year	Adult	Juvenile
1995–96	4:1	1:5
1996–97	2:1	3:11
1997–98	2:4	2:7
1998–99	1:5	2:4
Total: M	9 (45%)	8 (23%)
F	11 (55%)	27 (77%)

Table 7. Frequency of intraspecific perch displacement between and among different age and sex classes of Rough-legged Hawks wintering in the Mission Valley, Montana, 1997–99. Failed displacement attempts are shown in parentheses. Interactions involving one or both birds of unknown age and sex are excluded.

Displacer–Displaced	Frequency	Relative Frequency	% Failed
Adult female–Juv (unk sex)	39 (1)	32%	3%
Juv (unk sex)–Juv (unk sex)	25 (5)	20%	17%
Adult female–Adult female	23 (1)	19%	4%
Adult female–Adult male	16	13%	0%
Adult male–Juv (unk sex)	6	5%	0%
Juv (unk sex)–Adult female	6 (5)	5%	46%
Adult male–Adult male	4 (1)	3%	20%
Juv (unk sex)–Adult male	3 (1)	2%	25%
Adult male–Adult female	1	1%	—
Total	123 (14)	—	—

classes occurred more frequently. Juveniles failed when attempting to displace adult females and adult males 45% and 25% of the time, respectively, whereas adults rarely failed when attempting to displace juveniles (Table 7). When comparing the ratio of aggressive encounters won versus the total number of aggressive encounters for each age and sex class, we found adult females won 85% (N = 108) of interactions, compared with 42% for adult males (N = 33), 72% for juvenile females (N = 46) and 33% for juvenile males (N = 15). The mean occurrence-rate of aggressive intraspecific interactions was 0.387/hr (N = 17) over 384 total hours of observation.

Discussion

Our observations indicated that adult female Rough-legged Hawks tend to winter farther north than adult males, but that differential migration does not occur between adults and juveniles. Watson (1984) reported that 81% of all Rough-legged Hawks were adults and 69% of adults were males in his study site in southern Idaho (43°45′N, 112°45′W), which lies midway in latitude between our northern and southern study sites (Fig. 1). Watson's ratio of adult males to adult females was larger than that in Montana and smaller than that in California and Nevada, suggesting a latitudinal gradient in the distribution of the sexes. Additionally, Russell (1981) examined 42 male and 64 female specimens (adults and juveniles) collected between 10 December–14 February in the eastern United States (east of 104°W) and found that females wintered, on average, 3° farther north than males. Furthermore, Russell showed a clear gradient in sex ratio from north to south. When we combined this evidence with the sex ratios recorded for museum specimens in the western United States, a gradient from north to south, with predominantly females in the north and males in the south, appeared to be consistent (Table 5). Although certain biases can be introduced by using museum collections, the sex ratios were similar to those observed on road surveys at the same latitudes.

Because Russell (1981) did not distinguish adults from juveniles, it has remained largely unknown whether juveniles also exhibit differential migration between the sexes. Seventy-seven percent of juveniles trapped in the Mission Valley, Montana, during the winters of 1995–99 were females based on measurements. Moreover, the highest proportion of juvenile females occurred the same year that we observed the highest proportion of adult females on road surveys and the lowest densities of hawks. Differential trapability between sexes could bias the sex ratio of trapped birds; indeed, adult females tended to be more difficult to trap than adult males. However, if this pattern were true for juveniles, then the trapping ratios would underestimate rather than overestimate the proportion of juvenile females. Furthermore, juveniles are much more easily trapped than adults, and the likelihood of juvenile males being so consistently underrepresented seems small. Therefore, we concluded that the trapping data indicated that sex differences in winter distributions are similar for adults and juveniles.

Intraspecific interactions and territoriality in Rough-legged Hawks during winter are highly complex and poorly understood (Watson 1984, Bildstein 1987, Palmer 1988). Aggression and territoriality may change daily depending on weather (Temeles and Wellicome 1992), food availability, and a variety of other unknown factors (Watson 1984). Watson recorded the frequency of aggressive intraspecific interactions between known-sex Rough-legged Hawks wintering in Idaho and found that 70% of all interactions (N = 76) involved females displacing males. Watson (1984) did not distinguish between juveniles and adults, however. When separating the different age and sex classes, we found that adult females displaced adult males much more frequently. Additionally, adult females displaced other adult females more often than adult females displaced adult males, which differed greatly from Watson's (1984) findings in Idaho. When considering the success rate of displacement attempts and the overall success rate for each age and sex class, it appeared that adult females are the most dominant class and juvenile males are the least dominant. Interactions between adult males and juvenile females were more complicated and remain poorly understood. Two major differences between Watson's (1984) study site and the Montana study area, were that Rough-legged Hawks in Idaho frequently fed on road-killed carrion, whereas hawks in the Mission Valley rarely fed on carrion and foraged almost exclusively on small mammals (C. Olson unpubl. data) and the densities of Rough-legged Hawks were much higher in three of four years in the Mission Valley ($\bar{x}$ = 1.14 birds/km) than in Idaho ($\bar{x}$ = 0.18 birds/km; Watson 1984). It is unknown, however, how these factors influence the social interactions of Rough-legged Hawks during winter.

The ratio of juveniles to adults on the road surveys did not differ significantly within a season; however, the proportion of juveniles did vary among winters. Furthermore, the overall density of Rough-legged Hawks in Montana was considerably lower in the first winter than in the following three winters. The low numbers observed in the first winter followed a major decline in voles (*Microtus* spp.) in the area. Rough-legged Hawk numbers are known to fluctuate considerably (Baker and Brooks 1981, Mindell and White 1987, Palmer 1988, Virkkala 1992, Swem 1996, Potapov 1997), and fluctuations in the number of wintering juveniles are often attributed to changes in reproductive success prior to the subsequent winter (Bent 1937, Brown and Amadon 1968). However, a variety of local and regional factors such as prey availability, weather, and/or the presence of conspecifics, also may influence the distribution and density of wintering juveniles.

REVIEW OF HYPOTHESES

Based on the arrival-time hypothesis, we would expect the sex that establishes the breeding territory to winter farthest north. Several lines of evidence suggest that the arrival-time hypothesis does not apply to Rough-legged Hawks. First, males usually establish territories in most North American raptor species (Newton 1979, Johnsgard 1990), and hence we would expect to find a preponderance of adult males wintering farther north. Second, although not well-documented, Rough-legged Hawks are thought to arrive on the breeding grounds already paired (Bent 1937, Mindell *in* Palmer 1988). If pairs do arrive simultaneously, such behavior would be inconsistent with the arrival-time hypothesis. Finally, the arrival-time hypothesis would act predominately on breeding birds (Myers 1981), and because juvenile Rough-legged Hawks are not likely to breed in their first season, we would not expect similar latitudinal segregation among juveniles (Kjellén 1994).

The social-dominance hypothesis proposes that subordinate individuals are forced to winter farther south to avoid competition with dominant conspecifics (Gauthreaux 1985). Hence, the dominant sex would be expected to display aggressive behavior toward individuals of the opposite sex and/or subordinate age classes, especially in more northern wintering areas. In Rough-legged Hawks, the larger females should be dominant within each age class. Thus, according to the social-dominance hypothesis, adult females should winter farthest north, juvenile males farthest south, and adult males and juvenile females overlapping in the middle, depending on which class is most dominant (Kerlinger and Lein 1986).

Although it appears that adult female Rough-legged Hawks are dominant over the other classes, and juvenile males tend to be subordinate, it remains unclear whether juvenile females dominate adult males, or vice versa. Roughly 70% of behavioral interactions did not involve adult males. Conversely, 64% of interactions involved juveniles, suggesting that frequency of antagonistic interactions, alone, does not explain why Rough-legged Hawks exhibit differential migration by sex and not age. Although habitat segregation by sex has been attributed to social dominance in other species (Koplin 1973, Mills 1976), studies supporting the social-dominance hypothesis have failed to show that intraspecific competition, and not various environmental factors, results in the latitudinal segregation of the sexes.

If our data accurately reflect the sex ratios of juvenile hawks wintering in the Mission Valley, then they indicate that similar selection pressures are acting equally on adults and juveniles. If social dominance were the main operating factor, we would expect juvenile males to occur in lower proportions than adult males in the more northern areas. Furthermore, the sex ratio of adults should change as food availability decreases and/or as hawk densities change, as would be expected by the social-dominance hypothesis. However, the sex ratios changed very little between years of extremely low densities and presumably limited food (1995–96 pers. obs.), and extremely high wintering densities with abundant food (1998–99 pers. obs.) in Montana. Indeed, although Russell (1981) favored the social-dominance hypothesis for explaining differential migration by sex in Rough-legged Hawks, he suggested that the migration patterns may be flexible, varying as regional environmental conditions vary.

We propose that the most influential factor regulating differential winter distribution in the Rough-legged Hawk is thermoregulation and tolerance of more extreme winter conditions, i.e., the body-size hypothesis (Ketterson and Nolan 1976, Searcy 1980). In Montana, we detected the highest proportions of adult females on December and January surveys, and the highest proportions of adult males on the first and last surveys, during the two coldest winters (1995–96 and 1996–97). Moreover, the mean ratio of adult females to adult males in Montana was significantly inversely correlated with average temperature, and less-strongly correlated with average snowfall, among the four winters. Cade (1955) found no overlap in body mass between sexes of Rough-legged Hawks, although the sample sizes were small. When considering all morphological measurements, Cade and Palmer (1988) both estimated a minimum of 75% non-overlap between the sexes. So, female Rough-legged Hawks are clearly larger on average than males. Herreid and Kessel (1967) determined for 31 species of birds that larger individuals have relatively heavier plumage and more effective insulation than smaller birds. Finally, Root (1988) suggested that larger body size increases potential energy stores and therefore enables longer periods of fasting, and further claimed that energy constraints eventually limit the distribution and abundance of species. If this is true for Rough-legged Hawks, then females may be more capable than males of withstanding colder temperatures and fasting during periods of deep snow and low prey availability. Therefore, we believe thermoregulatory constraints may be an important factor contributing to the differential latitudinal winter distribution of the sexes in the Rough-legged Hawk. Because the predictions of the social-dominance hypothesis overlap with those of the body-size hypothesis, it is difficult to completely disprove one or the other hypothesis. Clearly, further research is needed on the differences between the sexes in thermal conductance and the behavioral differences among the ages and sexes in territoriality.

Other suggested possibilities explaining female hawks wintering farther north than males, include greater prey-switching capability, interspecific competition or both (T. Swem pers. comm.). Because females are larger overall, they should be more capable of switching to alternative prey-types during periods of deep snow and subsequently low prey availability. Rough-legged Hawks are recognized as small mammal specialists; however, a variety of small and medium birds have been recorded at nests (Swem 1996), and road-killed carrion was commonly fed upon in Idaho (Watson 1984). Although neither of these ideas was specifically examined in this study, Rough-legged Hawks were seen foraging almost exclusively on small mammals, even throughout periods of deep (>10 cm) snow cover (Olson unpubl. data). Additionally, interspecific competition involving prey was likely much less than observed with hawks feeding on carrion in Idaho, because of the smaller size, faster consumption times and overall greater abundances usually associated with small mammals as prey. Therefore, these potential benefits for the larger sex may be in addition to, but probably are not, the actual operating factors.

Finally, we expected a greater proportion of males in Montana early and late in the season, especially during migration. Although we observed the highest proportion of males during November and April, this was not significantly different from the rest of the winter. Russell (1981) also noted that sex ratios remained relatively unchanged during a winter. Thus, we suspect that migration, especially during fall, may be rapid and relatively continuous in birds wintering farther south, thereby explaining why we did not observe greater numbers of adult males stopping over in the Mission Valley during migration.

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